

- Cameron, K.M. and M.W. Chase. 1999. Phylogenetic relationships of Pogoniinae (Vanilloideae, Orchidaceae): an herbaceous example of the eastern North America – eastern Asia phytogeographic disjunction. *J. Plant Res.* 112: 317–329.
- Cameron, K.M., M.W. Chase, W.M. Whitten, P.J. Kores, D.C. Jarrell, V.A. Albert, T. Yukawa, H.G. Hills, and D.H. Goldman. 1999. A phylogenetic analysis of the Orchidaceae: evidence from *rbcL* nucleotide sequences. *Amer. J. Bot.* 86: 208–224.
- Cameron, K.M. and C. Molina. 2006. Photosystem II gene sequences of *psbB* and *psbC* clarify the phylogenetic position of *Vanilla* (Vanilloideae, Orchidaceae). *Cladistics* 22: 239–248.
- Chase, M.W., K.M. Cameron, R.L. Barrett, and J.V. Freudenstein. 2003. DNA data and Orchidaceae systematics: a new phylogenetic classification. Pp. 69–89 in K.W. Dixon, S.P. Kell, R.L. Barrett, and P.J. Cribb, eds. *Orchid Conservation. Natural History Publications*, Kota Kinabalu, Sabah, Malaysia.
- Cogniaux, A. 1904–1906. Orchidaceae. Pp. 1–604 in C.F.P. Martius, A.G. Eichler, and I. Urban, eds. *Flora Brasiliensis*, Volume III, Pars VI. R. Oldenbourg, Munich, Germany.
- Dressler, R.L. 1993. *Phylogeny and Classification of the Orchid Family*. Dioscorides Press, Portland, Oregon, USA.
- Edwall, G. 1903. Plantas paulistas novas ou menos conhecidas. *Revista Centro Sci. Campinas* 2: 191–195.
- Freudenstein, J.V., C. van den Berg, D.H. Goldman, P.J. Kores, M. Molvray, and M.W. Chase. 2004. An expanded plastid DNA phylogeny of Orchidaceae and analyses of jackknife branch support strategy. *Am. J. Bot.* 91: 149–157.
- Garay, L.A. 1986. *Olim Vanillaceae*. Bot. Mus. Leaflet 30: 223–237.
- Harris, J.G. and M.W. Harris. 1994. *Plant identification terminology: an illustrated glossary*. Spring Lake Publishing, Utah, USA.
- Hoehne, F.C. 1945. Orchidáceas. Pp. 1–389 (+209 Tabs.) in F.C. Hoehne, ed. *Flora Brasílica*, Fasc. 8 (Vol. XII, II; 13–43). Secretaria da Agricultura, Indústria e Comércio de São Paulo, São Paulo, Brazil.
- Pabst, G.F.J. and F. Dungs. 1975. *Orchidaceae Brasilienses*. Band I. Brücke-Verlag Kurt Schmiersow, Hildesheim, Germany.
- Pansarin, E.R. 2005. “Sistemática filogenética e biologia floral de Pogoniinae sul-americanas, e revisão taxonômica e análise das ceras epicuticulares do gênero *Cleistes* Rich. ex Lindl. (Orchidaceae).” Ph.D Thesis. Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.
- Pansarin, E.R. and F. Barros. 2008. Taxonomic notes on Pogoniinae (Orchidaceae): *Cleisteslopsis*, a new genus segregated from *Cleistes*, and description of two new South American species, *Cleistes batistana* and *C. elongata*. *Kew Bull.* 63: 441–448.
- Pansarin, E.R., A. Salatino, and M.L.F. Salatino. 2008. Phylogeny of South American Pogoniinae (Orchidaceae, Vanilloideae) based on sequences of nuclear ribosomal (ITS) and chloroplast (*psaB*, *rbcL*, *rps16*, and *trnL-F*) DNA with emphasis on *Cleistes* and discussion of biogeographic implications. *Org. Divers. Evol.* 8: 171–181.
- Stern, W.L. and W.S. Judd. 2000. Comparative anatomy and systematics of the orchid tribe Vanilleae excluding *Vanilla*. *Bot. J. Linn. Soc.* 134: 179–202.

## SPATIAL DISTRIBUTION AND ABUNDANCE OF EPIPHYTES ALONG A GRADIENT OF HUMAN DISTURBANCE IN AN INTERANDEAN DRY VALLEY, ECUADOR

FLORIAN A. WERNER\* AND S. ROBBERT GRADSTEIN

Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany. Email: florianwerner@yahoo.com

**ABSTRACT.** We studied the effects of different disturbance regimes on abundance and within-tree distribution of dry-forest epiphytes at the Bosque Protector Jerusalén in northern Ecuador. Epiphytes on 100 trees of *Acacia macracantha* were sampled in closed mixed and pure acacia forest stands, forest edge, semi-closed secondary woodland, and isolated trees in pastures. Vascular epiphytes were sampled for entire host trees and macrolichens and bryophytes for inner tree crowns. The number of vascular epiphyte species did not differ significantly between crown zones but their cover decreased significantly from middle to inner and outer crown. Vascular epiphytes attained greatest and bryophytes lowest cover values on isolated trees. Covers of bryophytes and vascular plants were correlated with canopy integrity, suggesting that microclimate was a strong predictor of epiphyte abundance. The high abundance of atmospheric bromeliads in the studied disturbed, perarid habitats is suggestive of their effective adaptation to the use of dew.

**Key words:** edge effects, isolated trees, microclimate, succession, tropical montane dry forest

### INTRODUCTION

Human disturbance may affect epiphyte diversity through a number of factors. Degraded and secondary forests usually offer less surface area for colonization than primary forests, with humus and bryophyte mats on old, thick limbs being particularly scarce (Acebey et al. 2003, Krömer & Gradstein 2003). Dispersal constraints may limit epiphyte diversity in fragmented habitats (Cascante-Marín et al. 2009), and altered microclimate may further affect their abundance (Sillett et al. 1995, Krömer & Gradstein 2003, Köster et al. in press). Disturbed forests are characterized by fragmented or lower and more open canopies that experience greater illumination and air turbulence and exhibit less stratification by microclimate compared to undisturbed forests (e.g., Malhi & Phillips 2004). Especially in secondary forests recovering from clear-cutting, time since disturbance is an additional factor that warrants attention, because epiphytes tend to grow slowly (e.g., Zotz 1995, Nadkarni et al. 2000) and their recolonization invariably lags behind that of their host trees.

Interestingly, there is little agreement among studies regarding how tropical epiphytes respond to human disturbance. Epiphyte diversity in altered habitats ranges from similar (Hietz & Hietz-Seifert 1996, Larrea 1997, Holz & Gradstein 2005) to substantially lower than in mature forests (Acebey et al. 2003, Krömer & Gradstein 2003, Benavides et al. 2006, Nöske et al. 2008). Epiphyte abundance in disturbed habitats differs

even more widely, ranging from significantly lower (Krömer & Gradstein 2003, Werner et al. 2005, Benavides et al. 2006) to significantly higher than in intact forest (Dunn 2000, Flores-Palacios & García-Franco 2004, Cascante 2006). However, even in cases where abundance increases, diversity may decrease (Dunn 2000, Flores-Palacios & García-Franco 2004, Cascante 2006), and these discrepancies are not understood.

Only a few studies have targeted dry-forest epiphytes, and none of them dealt with forest disturbance. Because dry compared to moist forest canopies tend to be more open, gradients of humidity and exposure are less pronounced there (Graham & Andrade 2004), and it seems conceivable that dry-forest epiphytes are relatively resilient to forest disturbance due to their high tolerance for drought. In a previous article (Werner & Gradstein 2009) we have treated the impact of different types and magnitudes of disturbance on species richness and floristic composition of epiphytes in a tropical montane dry forest. The present paper deals with epiphyte abundance and within-tree distribution in the same study system.

### METHODS

#### Study Site and Sampling

Field work was carried out between January and March 2004 at the Bosque Protector Jerusalén, a state reserve in the Interandean Guayllabamba watershed north of Quito, Ecuador. The reserve includes one of the least disturbed Interandean dry forests of the Ecuadorian Andes. The study site

\* Corresponding author.

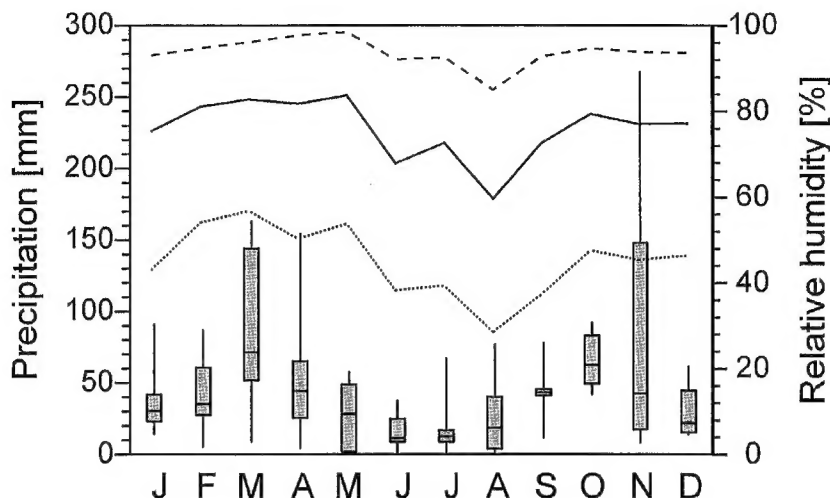


FIGURE 1. Precipitation and air humidity at Jerusalén. Rain (box-plots) for 1963–1972 (INAMHI 1964–1973). The lines are mean (solid), minimum (dotted) and maximum (dashed) daily air humidity 2 m above ground from April 2004 to April 2005 (original data).

was situated on a plateau at 2300–2320 m elevation (00°00'S, 078°21'W).

Rainfall data from Jerusalén is available for 1963–1972 (INAMHI 1964–1973). Mean annual precipitation is 530 mm with high inter-annual variability (FIGURE 1). The area experiences up to 12 arid months (Guerrón et al. 2005) and is characterized by a pronounced valley-mountain breeze typically picking up around noon; fog is uncommon (S. Reyes, pers. comm.).

We randomly sampled 20 canopy representatives (>25 cm trunk diameter at the point of lowest circumference) of the dominant local evergreen species, *Acacia macracantha* Humb. & Bonpl. ex. Willd. (FIGURE 2), in the following five habitat types:

1. **Closed Mixed Forest.** This forest type had the tallest canopy ( $8.0 \pm 1.3$  m SD); trunk diameter was  $35.8 \pm 11.3$  cm. Primary forest in the area has long disappeared as elsewhere in dry Interandean valleys (Fjeldsø 2002). Judging from aerial photographs (1992, 1976), this and the following forest type was ca. 50 years of age.
2. **Closed Acacia Forest.** This forest type closely resembled mixed forest in structure, but was composed exclusively by *A. macracantha*. Tree height and trunk diameter were  $6.3 \pm 1.2$  m and  $36.2 \pm 10.7$  cm, respectively.
3. **Forest Edge.** Edge habitat was defined as the first tree row of closed forest bordering open grasslands. Structurally, the edge trees closely resembled those located deeper in mature forest. Edges had been kept open for 13–28 years. Tree height and trunk diameter

were  $6.9 \pm 1.0$  m and  $39.2 \pm 10.0$  cm, respectively.

4. **Semi-closed Secondary Acacia Woodland.**

As indicated by aerial photographs, this vegetation type had been regenerating from pasture stocked with well-established isolated trees for ca. 20 years. Tree height and trunk diameter were  $5.4 \pm 0.9$  m and  $40.7 \pm 14.0$  cm, respectively.

5. **Isolated Trees.** These trees were markedly

different in stature from forest trees in having very short trunks, near-horizontal branches and dense, low, flat-topped, and wide-spreading crowns. This mode of growth is typically observed in absence of light competition, suggesting that these were not remnant trees but had established in grasslands. Isolated trees were located 12–2200 m (mean:  $537 \pm 592$  m) from closed forest. Tree height and trunk diameter were  $5.1 \pm 1.4$  m and  $44.0 \pm 15.7$  cm, respectively.

Sampling was conducted by climbing and from the ground, aided by a pair of Minox BD 42 × 10 binoculars. Trees were divided into four zones modified after Johansson (1974): trunk (Johansson Zone 1), major branches ('inner crown'; JZ 3), minor branches down to ca. 5 cm of diameter ('middle crown'; JZ 4) and twigs ('outer crown'; JZ 5). This scheme was adjusted for individual trees in such way as to yield three crown zones of roughly equivalent branch surface area. Trunks were short (ca. 1 m on average) and therefore invariably presented less surface area for epiphytes. Vascular epiphytes were recorded for each of the four zones, excluding the accidental species

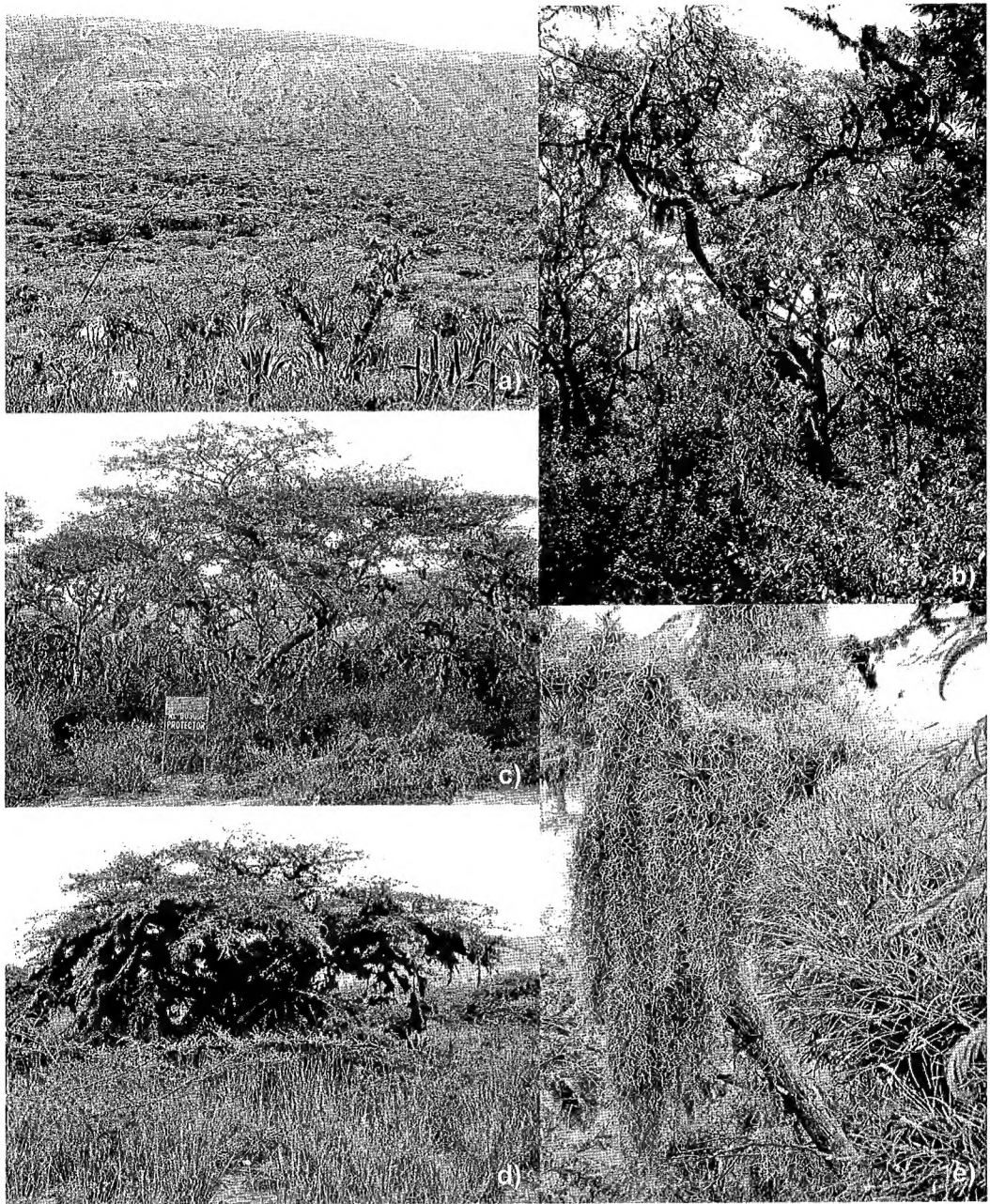


FIGURE 2. The study site, Bosque Protector Jerusalén. **a.** View of the core forest, with the Malchinguí escarpment in the background. **b.** Closed mixed forest. **c.** Forest edge. **d.** Isolated tree. **e.** Atmospheric *Tillandsia usneoides* (left), *T. recurvata* (right) and scattered juvenile *T. incarnata* (top left).

(sensu Benzing 1990). Three CAM-type atmospheric *Tillandsia* spp., most notably *T. recurvata*, were omnipresent with densities ranging from 1000–10,000 often tightly interwoven genets per tree. Consequently, counts of individuals or ‘stands’ were not feasible. Instead, we estimated

surface cover, which, for similar reasons, was also used as the measure of abundance for lichens and bryophytes. Vascular plant cover was estimated for each of the Johansson zones. Because bryophyte and macrolichen (foliose and fruticose lichens) abundance in the middle and outer canopy

TABLE 1. Spatial distribution (frequencies throughout Johansson-zones) of vascular epiphytes in five habitats (N = 20 trees).

Taxon	MF				AF				FE				SW				IT				Mean				
	1	3	4	5	1	3	4	5	1	3	4	5	1	3	4	5	1	3	4	5	1	3	4	5	
Bromeliaceae																									
<i>Racinaea fraseri</i>	—	—	1	2	—	—	—	1	1	—	—	—	—	—	—	1	6	—	1	2	3	—	—	—	2.4
<i>Tillandsia incarnata</i>	2	20	20	20	1	20	20	20	3	20	20	20	8	20	20	20	1	19	19	20	3.0	19.8	19.8	20.0	
<i>Tillandsia lajensis</i>	—	1	—	1	—	—	—	—	2	—	—	—	—	—	—	—	—	—	1	2	—	—	—	1.0	
<i>Tillandsia recurvata</i>	3	20	20	20	1	20	20	20	5	20	20	20	10	20	20	20	16	20	20	20	7.0	20.0	20.0	20.0	
<i>Tillandsia usneoides</i>	—	16	20	20	1	19	20	20	1	17	20	20	6	20	20	20	1	17	19	19	1.8	17.8	19.8	19.8	
Polypodiaceae																									
<i>Pleopeltis macrocarpa</i>	—	2	—	—	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	0.6	0.2	—
<i>Pleopeltis thysanolepis</i>	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—
<i>Polypodium murorum</i>	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—
Mean species number/tree	0.3	3.1	3.1	3.2	0.2	3.1	3.1	3.2	0.5	2.9	3.0	3.0	1.2	3.1	3.1	3.3	0.9	2.9	3.1	3.2	0.6	3.0	3.0	3.2	0.4
± standard deviation	0.6	0.7	0.2	0.4	0.5	0.4	0.2	0.4	0.8	0.4	0.0	0.0	1.2	0.2	0.2	0.5	0.6	0.6	0.6	0.6	0.9	0.5	0.3	0.4	—

<sup>a</sup> modified after Johanson 1974; JZ1=trunk; JZ3=inner crown; JZ4=middle crown; JZ5=outer crown.

<sup>b</sup> habitat types: MF=mature mixed forest; AF=mature acacia forest; FE=mature forest edge; SW=semi-closed woodland; IT=isolated trees.

could not be estimated accurately, their abundance was registered only for the inner crown. Covers were estimated in steps of 5% with two additional steps of 1 and 2% respectively. Because epiphyte assemblages were strongly dominated by small atmospheric *Tillandsia* spp. and short turfs and mats of bryophytes respectively, cover values should be strongly correlated with biomass.

As a measure of canopy integrity, the percentage of crown circumference contacting neighboring crowns ('crown closure') was estimated to the nearest 5% for each host tree.

### Analysis

Between-group differences were analyzed with a one-way analysis of covariance (ANCOVA) after log (vascular cover Z3, Z5), arcsine-root (vascular cover Z4, crown means [Z3-5]) and 1/squareroot transformation (bryophyte and lichen cover) respectively. Trunk diameter was added as a covariate to control for tree size, which influences measures of diversity and abundance through substrate age and area available for settlement (Flores-Palacios & García-Franco 2006). Where parametric assumptions could not be matched through transformation (vascular epiphytes in JZ 1), the Kruskal-Wallis test and subsequent Mann-Whitney *U*-tests were used to test for differences between groups. Multiple tests of significance were corrected for a table-wide false discovery rate (FDR) of  $P < 0.05$  according to the step-up procedure described by Benjamini and Hochberg (1995). Vascular epiphyte cover was correlated using the mean of the three crown zones (JZ3-5), omitting the trunk. Because trunks were generally very narrow (as small as 30 cm in many isolated trees), their suitability as a habitat for epiphytes appeared to be influenced primarily by height and density of the understory. Analyses were done with Statistica 6.0.

### RESULTS

Eight species of vascular epiphytes were growing on the surveyed trees. Where present, they showed similar spatial distributions throughout the five habitat types surveyed (data not shown; see Werner 2008). Two species of bromeliads, *Racinaea fraseri* (Baker) M.A. Spencer and L.B. Sm. and *Tillandsia lajensis*, occurred mostly in the outer crown whereas the three smaller, atmospheric species, *Tillandsia incarnata* Kunth, *T. recurvata* (L.) L. and *T. usneoides* (L.) L., were omnipresent throughout the crowns but less common on trunks (TABLE 1). Three species of ferns [*Pleopeltis macrocarpa* (Bory ex. Willd.) Kaulf., *P. thysanolepis* (A. Braun ex Klotzsch)



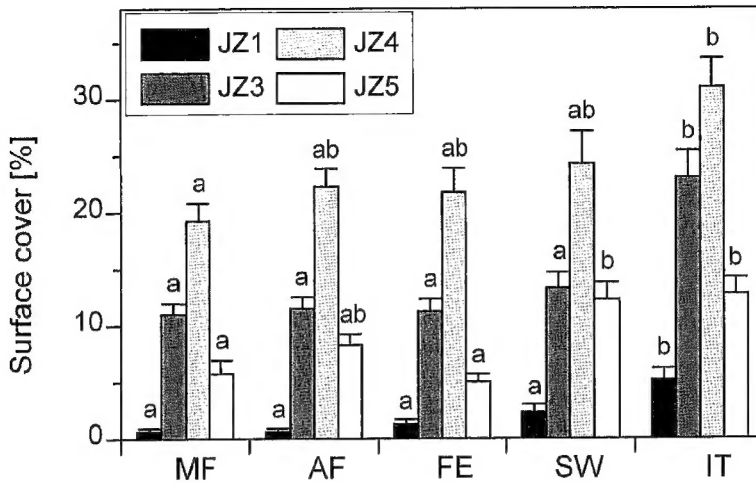


FIGURE 3. Spatial distribution of vascular epiphyte covers throughout habitat types. Shown are mean covers and standard errors for each Johansson zone (JZ). ANCOVA (JZ 3-5) and Kruskal-Wallis test (JZ 1) (all  $P < 0.005$ ;  $F_{5,94} = 11.31$  (JZ 3),  $F_{5,94} = 4.43$  (JZ 4),  $F_{5,94} = 8.21$  (JZ 5). Different letters indicate significant differences between habitat types (Scheffé test except in JZ 1 [U-test] at  $P < 0.05$  after FDR). MF=mature mixed forest; AF=mature acacia forest; FE=mature forest edge; SW=semi-closed woodland; IT=isolated trees.

E.G. Andrews and Wigham, and *Polypodium murorum* Hook.] were largely confined to the inner crown zone where they contributed less than 1% to total vascular epiphyte cover. Vascular species richness was similar in the crown zones but differed substantially on trunks, which were poorly colonized (TABLE 1). Species richness did not differ between habitats for any of the crown zones (all  $P > 0.1$ ;  $N = 20$ ; Kruskal-Wallis test).

The highest cover of vascular epiphytes occurred in the middle crown, while the lowest value was recorded on trunks across all of the habitat types. Pairwise comparisons showed significant differences between all of the Johansson-zones (all  $P < 0.001$ ;  $N = 100$ ; Wilcoxon test). For all of the Johansson-zones, vascular epiphyte cover tended to be highest on isolated trees. For trunk and inner crown, vascular plant cover on isolated trees was significantly higher than in any woodland habitat (FIGURE 3). Macrolichen cover was highest in forest edge and lowest in semi-closed woodland sites. Bryophyte cover ranged widely from  $17 \pm 10\%$  (mean  $\pm$  SD) in closed mixed forest to  $1 \pm 1\%$  on isolated trees (FIGURE 4). In semi-closed woodland, bryophyte cover was similar to closed forest, but significantly lower in forest edge (FIGURE 4).

Bryophyte cover was correlated positively with crown closure (Spearman's  $r_s = 0.66$ ,  $N = 100$ ,  $P < 0.001$ ), whereas vascular plant cover showed a weak negative correlation ( $r_s = 0.44$ ,  $N = 100$ ,  $P < 0.001$ ; FIGURE 5). Lichen cover, in contrast, was not correlated with crown closure ( $r_s = 0.00$ ,  $N = 100$ ,  $P > 0.5$ ; FIGURE 5).

## DISCUSSION

### Patterns of Epiphyte Frequency and Abundance

Differences in the ecotolerances of the two groups probably explain why macrolichen cover substantially exceeded bryophyte cover in all of the habitats. While most bryophytes demand shade and high humidity (Gradstein et al. 2001), many lichens favor full sunlight and frequent desiccation (Sipman & Harris 1989). The great abundance of bromeliads in the study area, especially of atmospheric *tillandsias*, is common in arid neotropical sites (Pedrotti et al. 1988, Ibisch 1996, Bernal et al. 2005, Reyes-García et al. 2008).

While the abundances and species numbers of vascular epiphytes in moist forests typically increases markedly from outer towards inner crown (Schimper 1888, Johansson 1974, Nadkarni 1984, Rudolph et al. 1998, Freiberg & Freiberg 2000), this was not the case at Jerusalén (FIGURE 3). The fact that bromeliad abundance decreased from middle to inner crown indicates a xerophilous character of the local bromeliads, which constituted all common vascular species and accounted for the bulk of epiphyte cover. Although their cover was highest in the middle crown, small twigs (outer canopy) clearly showed the highest incidents of bromeliad establishment judging by the numbers of seedlings present (compare Bernal et al. 2005). Dead remains of mature atmospheric *tillandsias* were conspicuously common in the inner crown (F. Werner pers. obs.), indicating that major limbs offer less

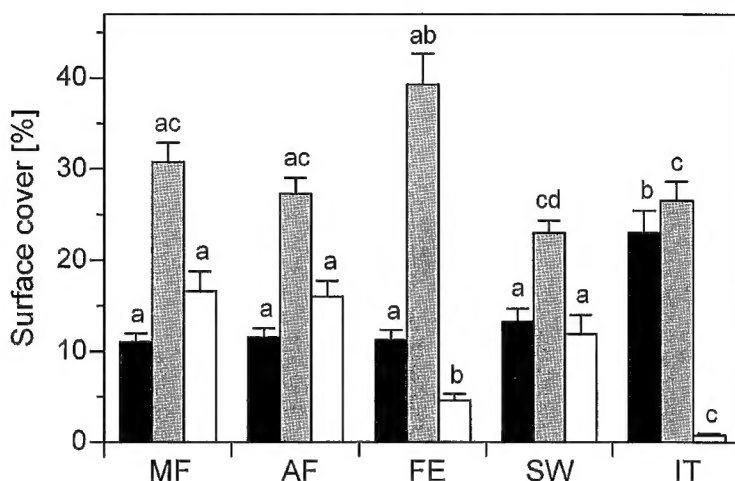


FIGURE 4. Inner-crown covers of vascular plants (black), lichens (grey) and bryophytes (white) throughout habitat types (means and standard errors). ANCOVA (all  $P < 0.001$ ):  $F_{5,94} = 11.31$  (vascular plants),  $F_{5,94} = 6.48$  (lichens);  $F_{5,94} = 48.11$  (bryophytes). Different letters indicate significant differences among habitat types (Scheffé test at  $P < 0.05$  after FDR). Habitat abbreviations as in Figure 3.

favourable conditions for the persistence of these plants as they become more shaded with time.

The xerophilous nature of bromeliads was also reflected by their habitat preferences. Highest covers of vascular epiphytes (essentially bromeliads) were consistently found on isolated trees. Increased bromeliad abundance or biomass on greatly exposed trees has often been observed (Bartoli et al. 1993, Caldíz & Fernández 1995, Hietz-Seifert et al. 1996, Dunn 2000, Cascante 2006). These trees apparently favor shade-intolerant *Tillandsia* species which, in denser forest, are confined to the uppermost canopy (Pittendrigh 1948, Flores-Palacios & García-Franco 2004).

#### Processes

The low incidences of bryophytes and ferns in disturbed habitats can not be explained by low substrate quantity or quality, given the similar sizes of sampled tree crowns, and their same-species identities. Instead, our results suggest a critical influence of altered microclimate on bryophyte performance following disturbance. Bryophyte cover was correlated negatively with crown closure, a proxy for canopy cover, and these cover changes were closely paralleled by bryophyte species richness and composition (Werner & Gradstein 2009).

All ferns and bryophytes at Jerusalén were clearly desiccation-tolerant and were usually encountered in the desiccated state (F. Werner pers. obs.). It seems curious that these desiccation-tolerant taxa were relatively scarce and exhibited a more mesic distribution than the desiccation-

intolerant *tillandsias*. This pattern may be due to differences in the usability of dew, which is an important source of moisture in arid regions (Andrade 2003), and here particularly in the outer canopy (Barradas & Glez-Medellín 1999). By means of highly evolved trichomes, atmospheric bromeliads make efficient use of this resource while effectively controlling water losses (Reyes-García et al. 2008). Although dew is also of potential benefit to bryophytes and ferns, periods of wetting from dew may often be too short to compensate for respiratory losses during tissue rehydration. Even xerophytic bryophytes require photosynthetic activity in the range of several hours to compensate for respiratory losses during rehydration (Alpert & Oechel 1985). However, the same adaptation that allows the success of atmospheric bromeliads under xeric conditions also helps limiting their performance in shade. Trichomes of the type that cover the foliage of bromeliads like *Tillandsia recurvata* promote water balance in dry habitats, but being highly reflective when dry, they prohibit success in shade. While moist, they further inhibit gas exchange and increase the incidence of fungal and bacterial infections (Martin 1994).

In conclusion, results from our analysis supports substantial shifts in the abundance patterns of epiphytic bryophytes and vascular plants, but not of macrolichens, from closed-canopy to disturbed montane dry forest. These results suggest that microclimate is a strong predictor for dry forest epiphyte distribution both within single trees and along the disturbance gradient under study. The high abundance of atmospheric bromeliads in the

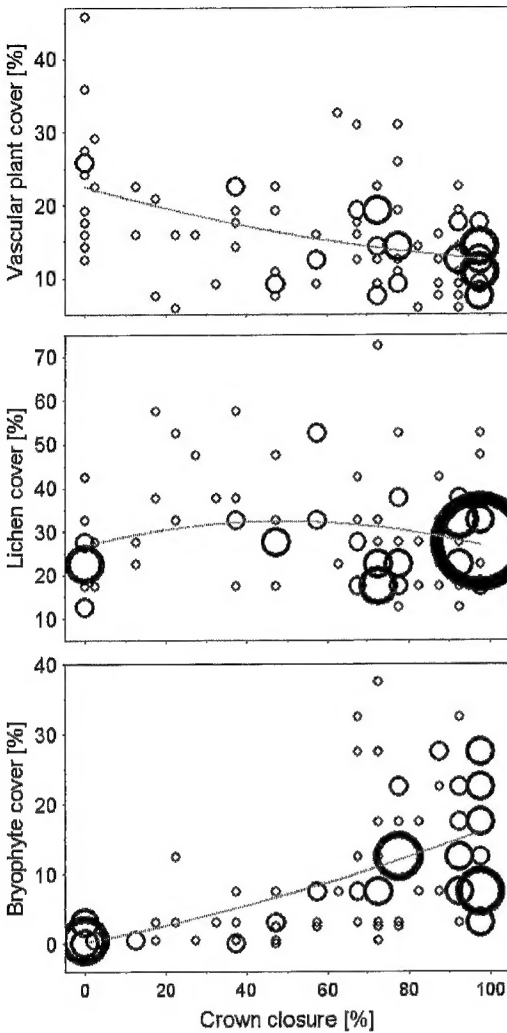


FIGURE 5. Relation between crown closure and the cover of bryophytes, lichens (inner crown) and vascular plants (crown means) respectively. Bubbles represent 1–10 host trees according to their size. Lines reflect polynomial fit (2<sup>nd</sup> degree).

studied disturbed, perarid habitats is suggestive of their effective adaptation to the use of dew.

#### ACKNOWLEDGEMENTS

We thank Don P. Jacome and the staff at Bosque Protector Jerusalén for their hospitality and support, especially M. Guerrón, P. Moncayo, J. Puga and S. Reyes. We gratefully acknowledge the support by the German Academic Exchange Service (DAAD), German Research Foundation (DFG), Idea Wild and Minox Optics. This is publication no. 212 of the Yanayacu Natural History Research Group.

#### LITERATURE CITED

- Acebey, A., S.R. Gradstein and T. Krömer. 2003. Species richness and habitat diversification of corticolous bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 18: 9–18.
- Alpert, P. and W.C. Oechel. 1985. Carbon balance limits the distribution of *Grimmia laevigata*, a desiccation-tolerant plant. *Ecol.* 66: 660–669.
- Andrade, J.L. 2003. Dew deposition on epiphytic bromeliad leaves: an important event in a Mexican tropical dry deciduous forest. *J. Trop. Ecol.* 19: 479–488.
- Barradas, V.L. and M.G. Glez-Medellín. 1999. Dew and its effects on two heliophile understory species of a tropical dry deciduous forest in Mexico. *Int. J. Biometeorology* 43: 1–7.
- Bartoli, C.G., J. Beltrano, L.V. Fernández and D.O. Caldíz. 1993. Control of the epiphytic weeds *Tillandsia recurvata* and *Tillandsia aëranthos* with different herbicides. *For. Ecol. Manage.* 59: 289–294.
- Benavides, A.-M., J.H.D. Wolf and J.F. Duivenvoorden. 2006. Recovery and succession of epiphytes in upper Amazonian fallows. *J. Trop. Ecol.* 22: 705–717.
- Benjamini, Y. and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. Roy. Stat. Soc. Ser. B.* 57: 289–300.
- Benzing, D.H. 1990. Vascular epiphytes: general biology and related biota. Cambridge University Press, Cambridge.
- Bernal, R., T. Valverde and L. Hernández-Rosas. 2005. Habitat preference of the epiphyte *Tillandsia recurvata* (Bromeliaceae) in a semi-desert environment in Central Mexico. *Can. J. Bot.* 83: 1238–1247.
- Caldíz, D.O. and L.V. Fernández. 1995. The role of the epiphyte weeds *Tillandsia recurvata* and *Tillandsia aëranthos* in native rural and urban forest. *Int. J. Ecol. Environ. Sci.* 21: 177–197.
- Cascante, A.M. 2006. Epiphytic bromeliad communities during premontane forest succession in Costa Rica. Ph.D. diss., Univ. Amsterdam, Netherlands.
- Cascante-Marín, A., N. von Meijenfeldt, H.M.H. de Leeuw, J.H.D. Wolf, J.G.B. Ostermeijer and J.C.M. den Nijs. 2009. Dispersal limitation in epiphytic bromeliad communities in a Costa Rican fragmented montane landscape. *J. Trop. Ecol.* 25: 63–73.
- Dunn, R.R. 2000. Bromeliad communities in isolated trees and three successional stages of an Andean cloud forest in Ecuador. *Selbyana* 21: 137–143.
- Fjeldsø, J. 2002. *Polylepis* forests—vestiges of a vanishing ecosystem in the Andes. *Ecotropica* 8: 111–123.
- Flores-Palacios, A. and J.G. García-Franco. 2004. Effects of isolation on the structure and nutrient content of oak epiphyte communities. *Plant Ecol.* 173: 259–269.
- . 2006. The relationship between tree size and epiphyte species richness: testing four different hypotheses. *J. Biogeogr.* 30: 323–330.
- Freiberg, M. and E. Freiberg. 2000. Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. *Journal of Tropical Ecology* 16: 673–688.



- Gradstein, S.R., S.P. Churchill and N. Salazar Allen. 2001. Guide to the Bryophytes of Tropical America. Memoirs of the New York Botanical Garden 86: 577 pp.
- Graham, E.A. and J.L. Andrade. 2004. Drought tolerance associated with vertical stratification of two co-occurring epiphytic bromeliads in a tropical dry forest. *American J. Bot.* 91: 699–706.
- Guerrón, M., A. Orellana, A. Looor and J. Zambrano. 2005. Estudio del Bosque Seco en el Bosque Protector Jerusalem. *Lyonia* 8: 5–18.
- Hietz-Seifert, U., P. Hietz and S. Guevara. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. *Biol. Conserv.* 75: 103–111.
- Holz, I. and S.R. Gradstein. 2005. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica—species richness, community composition and ecology. *Plant Ecol.* 178: 89–109.
- Ibisch, P. 1996. Neotropische Epiphytendiversität—das Beispiel Bolivien. Ph.D. dissertation, Universität Bonn. Martina Galunder-Verlag, Wiehl.
- INAMHI, 1964–1973. Manual meteorológico. Instituto Nacional de Meteorología y Hidrología del Ecuador, Quito.
- Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr. Suec.* 59: 1–136. Uppsala.
- Köster, N., K. Friedrich, J. Nieder and W.B. Barthlott. 2009. Conservation of epiphyte diversity in an Andean landscape transformed by human land use. *Conserv. Biol.* 23: 911–919.
- Krömer, T. and S.R. Gradstein. 2003. Species richness of vascular epiphytes in two primary forests and fallows in the Bolivian Andes. *Selbyana* 24: 190–195.
- Larrea, M. 1997. Respuesta de las epífitas vasculares a diferentes formas de manejo del bosque nublado, Bosque Protegido Sierrazul, zona de amortiguamiento de la Reserva Ecológica Cayambe-Coca, Napo, Ecuador. Pp. 321–346 in P.A. Mena, A. Soldi, R. Alarcón, C. Chiriboga and L. Suárez, eds. *Estudios Biológicos para la conservación*. EcoCien- cia, Quito.
- Malhi, Y. and O.L. Phillips. 2004. Tropical forests and global atmospheric change: a synthesis. *Phil. Trans. Roy. Soc. Lond. B* 359: 549–555.
- Martin, C.E. 1994. Physiological ecology of the Bromeliaceae. *Bot. Rev.* 60: 1–82.
- Nadkarni, N.M. 1984. Epiphyte biomass and nutrient capital of a neotropical rainforest. *Biotropica* 16: 249–256.
- . 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. *Biotropica* 32: 358–363.
- Nöske N.M., N. Hilt, F.A. Werner, G. Brehm, K. Fiedler, H.J.M. Sipman and S.R. Gradstein. 2008. Disturbance effects on epiphytes and moths in a montane forest in Ecuador. *Bas. Appl. Ecol.* 9: 4–12.
- Pedrotti, F., R. Venanzoni and E. Suárez Tapia. 1988. Comunidades vegetales del Valle de Capinota (Cochabamba – Bolivia). *Ecología de Bolivia* 11: 25–45.
- Pittendrigh, C.S. 1948. The bromeliad-*Anopheles*-malaria complex in Trinidad. I. The bromeliad flora. *Evolution* 2: 58–89.
- Reyes-García, C., H. Griffiths, E. Rincón and P. Huante. 2008. Niche Differentiation in Tank and Atmospheric Epiphytic Bromeliads of a Seasonally Dry Forest. *Biotropica* 40: 168–175.
- Rudolph, D., G. Rauer, J. Nieder and W. Barthlott. 1998. Distributional patterns of epiphytes in the canopy and phorophyte characteristics in a western Andean rain forest in Ecuador. *Selbyana* 19: 27–33.
- Schimper, A.F.W. 1888. Die epiphytische Vegetation Amerikas. *Botanische Mittheilungen aus den Tropen II*. Verlag Gustav Fischer, Jena.
- Sillett, S.C., S.R. Gradstein and D. Griffin. 1995. Bryophyte diversity of *Ficus* tree crowns from cloud forest and pasture in Costa Rica. *Bryologist* 98: 251–260.
- Sipman, H.J. and R.C. Harris. 1989. Lichens. Pp. 303–310 in H. Lieth and M.J.A. Werger, eds. *Tropical rainforest ecosystems*. Elsevier, Amsterdam.
- Werner, F.A. 2008. Effects of human disturbance on epiphyte assemblages in the Andes of Ecuador. Ph.D. diss., Univ. Göttingen, Germany.
- Werner, F.A. and S.R. Gradstein. 2009. Diversity of dry forest epiphytes across a gradient of human disturbance in the tropical Andes. *J. Veg. Sci.*
- Werner, F.A., J. Homeier and S.R. Gradstein. 2005. Diversity of vascular epiphytes on isolated remnant trees in the montane forest belt of southern Ecuador. *Ecotropica* 11: 21–40.
- Zotz, G. 1995. How fast does an epiphyte grow? *Selbyana* 16: 150–154.

## POLLINATION OF *NEMATANTHUS BRASILIENSIS*: AN EPIPHYTIC GESNERIACEAE ENDEMIC TO THE SOUTHEASTERN ATLANTIC FORESTS OF BRAZIL

IVONNE SANMARTIN-GAJARDO\*

Fundação Oswaldo Cruz, Programa de Implantação do Campus Fiocruz da Mata Atlântica, Av. Sampaio Correia 1A, Taquara, CEP 22713-374, Rio de Janeiro, Brasil. Email: icgajardo@gmail.com

JOSÉ RENATO SANTANA VIANNA

Centro Sócio Ambiental, Instituto de Pesquisa Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão 915, Jardim Botânico, CEP 22460-030, Rio de Janeiro, Brasil.

**ABSTRACT.** The floral biology and visitors of *Nematanthus brasiliensis* were studied in a submontane rainforest in Mangaratiba, Rio de Janeiro, Brazil. This species presents a flowering peak between October and February. Its flowers usually last eight days and show marked protandry. The floral features of *N. brasiliensis* suggest an ornithophilous pollination syndrome: tubular shape, pendent position, brightly colored, absence of perceptible odors. Nectar volume (21.3  $\mu$ l) and sugar concentration (31.8%) are also indicative of bird pollination. Field observations have verified this hypothesis: the flowers of *N. brasiliensis* are visited by two hummingbird species, *Ramphodon naevius* and *Phaetornis ruber*. Our data show that *P. naevius* is the main pollinator of *N. brasiliensis* and that it promotes cross-pollination. In addition, configuration of the reproductive structure in *N. brasiliensis* may avoid inter-specific pollen competition in style.

**Key words:** *Nematanthus*, floral biology, hummingbird pollination, *Ramphodon naevius*, pollinator behavior

### INTRODUCTION

Gesneriaceae is a moderate-size plant family comprising more than 3500 species in 140–150 genera, distributed mainly in the tropics (Weber 2004). In Brazil, 25 genera and about 230 species of gesneriads are found, occurring mostly in rain forests in the Amazonia region and along the Atlantic coast (Souza & Lorenzi 2005, A. Chautems pers. comm.). Wiehler (1983) estimated that about 60% of the Neotropical Gesneriaceae is hummingbird-pollinated, and it is an important source of nectar for hummingbirds in southeastern Brazil (Snow & Teixeira 1982, Buzato et al. 2000).

Inhabiting the coastal rain forest in Brazil, 31 species have been recognized for the genus *Nematanthus*, all characterized by their epiphytic and sometimes lithophytic habit (Chautems et al. 2005). Due to their brightly colored flowers, species of *Nematanthus* are commonly used as ornamental plants and several species have been introduced into cultivation in the US and Europe (Arnold 1978). Flowers with ornithophilous pollination syndrome (cf. Faegri & van der Pijl 1980) are a common feature for this genus, although three recently described species with large funnel-shaped white flowers exhibit a melittophilous pollination syndrome (Chautems et al. 2005).

*Nematanthus brasiliensis* (Vell.) Chautems is an epiphytic shrub restricted to a small stretch of

Atlantic coastal rain forest around the border of the São Paulo and Rio de Janeiro states, between 50 and 1200 meters (Chautems & Kiyama 2003). Its pendent flowers present brightly colored corollas that are tubular to cylindrical, suggesting that this species is hummingbird-pollinated. So far, effective visitors have been confirmed by fieldwork for the following six other species of *Nematanthus*: *N. fritschii* (Franco & Buzato 1992), *N. fissus*, *N. fluminensis*, *N. fornicis*, and *N. sericeus* (Buzato et al. 2000). In this paper we add to this body of knowledge in presenting descriptions of the floral biology of *N. brasiliensis*, as well as observations on the behavior of its visitors, especially of *Ramphodon naevius*, thought to be its effective pollinator.

### MATERIAL AND METHODS

Fieldwork was conducted from August 2004 to February 2005 and included observations in four populations along the North side of the river Rio Grande, in the Reserva Ecológica Rio das Pedras, a private ecological reserve (RPPN) that belongs to Club Mediterranée, in the Mangaratiba district (22°59'S 44°05'W, 30 m elevation), Rio de Janeiro, Brazil. Annual average temperature is 22°C and annual rainfall reaches 1200 to 2500 mm, with a wet season from December to February (Mynssen & Windisch 2004).

The flowers were observed in-situ to determine floral longevity and phases of anthesis. Effective

\* Corresponding author.